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Subtropical species of *Sinningia* (Gesneriaceae): Distribution patterns and limiting environmental factors

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ABSTRACT

The neotropical genus *Sinningia* Nees encompasses tuberous herbs or subshrubs which occupy a wide range of environments with respect to climate and soil or substrate types. The genus has more than 70 species distributed from Southern Mexico to Northern Argentina, with a diversity centre in the Brazilian Atlantic Rainforest. In this ecosystem, a large number of species occur in several particular vegetation types, occupying terrestrial, rupestrial and epiphytic substrates. The aims of this study were to describe the distribution patterns of subtropical *Sinningia* species, and to determine possible limiting factors for their range extension. We summarized environmental data for 21 subtropical species. Ten geographical and ecological variables were subdivided into several regional or local conditions. The occurrence of species in each of these conditions was obtained from published material, herbarium reviews and field expeditions. We used exploratory multivariate approaches, (cluster and ordination analyses) to assess the contribution of these variables to species' ecological and geographical distributions. Comparisons between groups of species were evaluated using randomization tests. Two major patterns of geographic distribution were identified for subtropical *Sinningia* species: widespread and restricted. Species richness according to spatial and climatic variables showed four distinct patterns. Habitat tolerance of the species also distinguished two groups in a wider continuum context. Cluster analysis resulted in two stable groups, which coincided almost entirely with an a priori classification based on geographic range. Ordination analysis showed a distinction between widespread and restricted species, as well as a gradient of substrate occupancy. Patterns of ecological and geographical distribution were strongly related to the evolutionary history of the genus. The southern distribution limit of *Sinningia* is mainly linked to shifts in vegetation types around the 30°S parallel, where the northern forested Atlantic and Paranean biogeographic provinces give place to the southern non-forested Espinal and Pampean provinces.

1. Introduction

Sinningia Nees is a Neotropical genus of the family Gesneriaceae with more than 70 species (Perret et al., 2006). The species of the genus are tuberous herbs or subshrubs, standing out for the variability of environments or substrates they occupy. Different species have specialized in a vast array of habitats: closed vegetation types such as pluvial, seasonal and montane forests, and more open dune forests (*restingas*), savannahs, lowland and montane grasslands, marshes and peat bogs, and rocky outcrop vegetation. Regarding substrate, species can be terrestrial, rupestrial, and/or epiphytic (Chautems et al., 2010; Ferreira et al., 2014; Araújo et al., 2015).

Sinningia is presently inserted in tribe Gesnerieae, subtribe Ligeriinae (Weber et al., 2013), along with *Paliavana* Vandelli and *Vanhouttea* Lemaire. The probable origin of *Sinningia* was a vicariant event with an ancestral taxon from the Amazon Forest that dates back around 30 Mya (Perret et al., 2013). However, *Sinningia* is a paraphyletic genus (Perret et al., 2003) and a new generic circumscription will be probably proposed in the near future.

The genus is distributed from Southern Mexico to Northern Argentina, with a diversity centre in the Brazilian Atlantic Rainforest (Wiehler, 1983; Chautems et al., 2010; Perret et al., 2006; Araújo et al., 2015). The greatest diversity of *Sinningia* is found along

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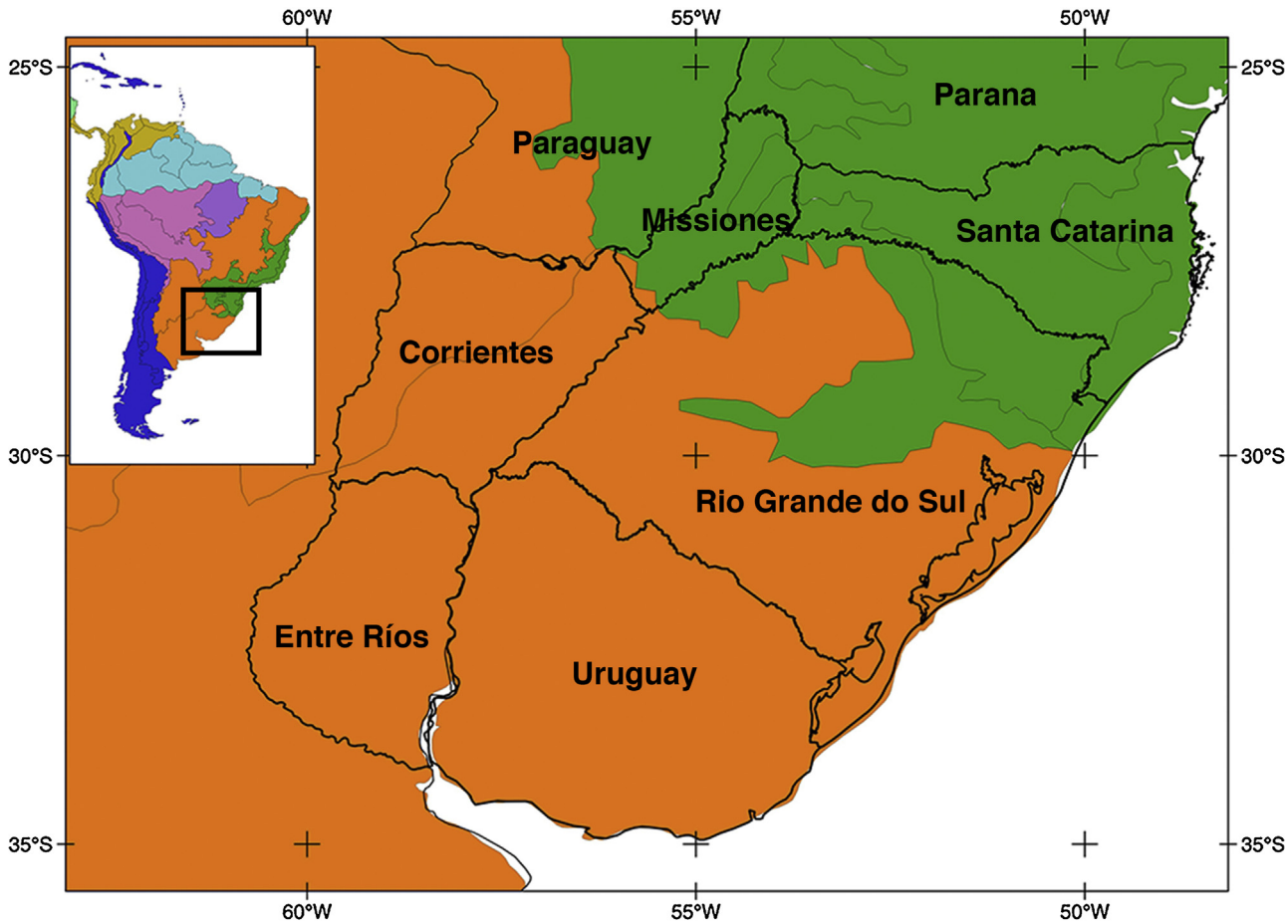

Fig. 1. The study area as circumscribed by ecotone region along six political areas in southern Brazil, northeastern Argentina and Uruguay. Green: humid and forested region of Amazon domain; Orange: driest and shrubby region the of the Chacoan domain.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mountain ranges within the Atlantic Rainforest. A lower number of species also occurs in areas with seasonal vegetation, such as the semi-deciduous forests of the Paraná-Paraguay river basin, the cerrados of central Brazil, and the caatingas of northeastern Brazil (Chautems, 2008; Perret et al., 2013).

The subtropical *Sinningia* species belong to two lineages, *Dircaea* and *Corytholoma*, which probably originated in the northeastern region of the Brazilian Atlantic Rainforest. The *Dircaea* clade has diversified in the Paraná River basin area, whereas the *Corytholoma* clade occurs in the north of the Tropic of Capricorn within the northern Atlantic Rainforest and the São Francisco River basin (Perret et al., 2006). The southward migration of *Corytholoma* and the northward migration of *Dircaea* may have been interrupted by an ecophysiological barrier, such as an area with very low rainfall, which has been described as a driver of floristic differences along the Brazilian Atlantic Rainforest (Brown, 1987; Oliveira-Filho and Fontes, 2000; Behling and Negrelle, 2001; Perret et al., 2006).

In order to better understand the biogeographic history of a given taxonomic group it is convenient to integrate knowledge on phylogenetic relationships and ecological characteristics. However, few biogeographic studies have in fact addressed these two points simultaneously (Huggett, 2004; Wiens and Donoghue, 2004). The aim of this paper was to answer three major questions: (i) how are *Sinningia* species distributed in eastern subtropical South America? (ii) do distribution ranges of species define regional centres of endemism? (iii) which ecological and/or geographical factors are limiting the occurrence of subtropical species?

2. Materials and methods

2.1. Study area

We defined our study area as a subtropical ecotone region between forest and grassland-dominated landscapes. This region comprised the two southernmost states of Brazil, Santa Catarina and Rio Grande do Sul, plus the three northeastern provinces of Argentina, Misiones, Corrientes and Entre Rios, eastern Paraguay and Uruguay. This area totals to ca. 820,000 km^2 and lies roughly between 25 and 35°S, which is often considered the limit for subtropical latitudes (Soriano et al., 1989), and is the transitional area between the more humid and forested Amazonian domain and the drier and non-forested Chacoan domain (Fig. 1), mostly comprising grasslands and parklands. The western limit is naturally defined by the course of the Paraná River.

Climate types in the region, according to the Köppen-Geiger system, are moist subtropical (*Cfa*) in the lowlands, and submontane areas and mild temperate (*Cfb*) in the higher elevations above 800 m (Peel et al., 2007). Temperatures show a strong seasonal variation, from hot summers in continental plains to moderate or relatively severe winters in montane areas, where up to 30 annual frost days and occasional snowfall. Mean annual temperature varies between 15 and 18 °C, with a minimum around −10 °C and a maximum around 40 °C (Moreno, 1961; Nimer, 1990; Hijmans et al., 2005).

Vegetation types in the region may be roughly divided into grassland and forest-dominated formations. More specifically, the

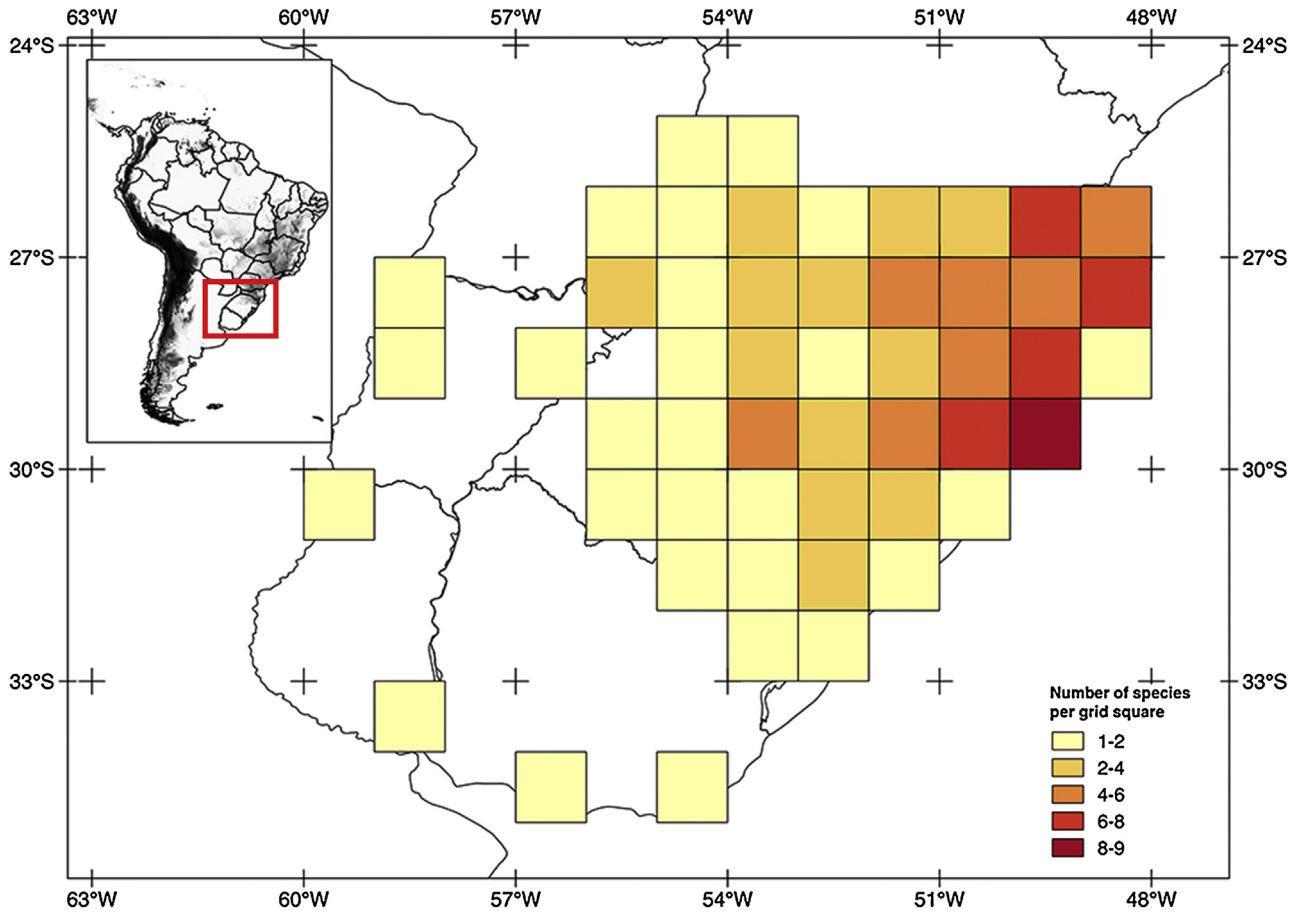

Fig. 2. Distribution and species richness of subtropical *Sinningia* species in southeastern South America.

area comprises three major formations: forests (Atlantic Rainforests, seasonal dry forests, and montane *Araucaria* forests), grasslands (northern montane grasslands and southern Pampas with gallery forests) and parklands ("palmares" or palm savannahs and "espinales" or thorn savannahs).

Atlantic Rainforests are essentially coastal ecosystems influenced by orographic rainfall along the Atlantic slopes of the Serra Geral mountain range. This formation occurs along the entire coastal region in Santa Catarina and extends to northeast Rio Grande do Sul, where it reaches its southern limit (Rambo, 1961). Seasonal dry forests are mostly inland formations, subjected to greater temperature than precipitation variations along the year. Seasonality in these forests is manifested by a greater diversity and abundance of deciduous species, mainly of the legume family (Rambo, 1951, 1954; Spichiger et al., 2004). *Araucaria* forests occur in higher elevations of the South Brazilian Plateau and are thus characterized by a higher proportion of temperate floristic elements (both Holarctic and Antarctic), especially the conifers *Araucaria* and *Podocarpus* (Rambo, 1951; Prado, 2000).

South Brazilian grasslands, collectively defined as *Campos* (Overbeck et al., 2007), are commonly divided into two major occurrence areas, the northern montane grasslands of the Paranean biogeographic province and the southern grasslands of the Pampean biogeographic province, mostly on lower elevations (Cabrera and Willink, 1980). Both areas of grasslands extend beyond the limits of South Brazil, the former to the Southeast and Northeast regions (Longhi-Wagner et al., 2012) and the later to Uruguay and the northeast provinces of Argentina, comprising an area known as the Rio de La Plata Grasslands (Soriano et al., 1989; Bilenca and Miñarro, 2004). Parklands are mostly southern grasslands with scattered palms of the genus *Butia* or spiny legumes of the genus *Prosopis* (Cabrera and Willink, 1980).

2.2. Data collection

Data regarding distribution and environment of *Sinningia* species were obtained from three information sources: (1) published material; (2) herbarium exsiccates; and (3) field expeditions. The bibliographical research focused mainly on floristic databases such as the Species List of the Brazilian Flora (Araujo et al., 2015), the Flora del Conosur (Chautems, 2008) and the Global Biodiversity Information Facility – GBIF database. We consulted the following herbaria: B, G, G-DC, HAS, HBR, HPL, HUCS, ICN, K, MBM, PACA, US and R. The ecogeographical data on herbarium labels were summarized in a data matrix. Additionally, field expeditions were conducted from September 2010 to November 2013.

Climatic data were obtained from Worldclim database (Hijmans et al., 2005). Rock and soil types follow the database of Environmental Data Explorer (available at http://geodata.grid.unep.ch/) and DIVA-GIS (available at http://www.diva-gis.org/Data). Vegetation types follow broadly recognized formations in publications on Brazilian and South American biogeographic systems (e.g. Cabrera and Willink, 1980; Morrone, 2001). The occurrence of each species was plotted on maps using Quantum GIS software (QGis DT, 2013), overlapping the ecogeographical data. To estimate the extent of occurrence we used the GeoCat software of the Royal Botanical Garden, Kew (Bachman et al., 2011).

To determine limiting factors for the extension range of *Sinningia* species we summarized information from 10 factorial variables in a data matrix. At a regional scale these variables can

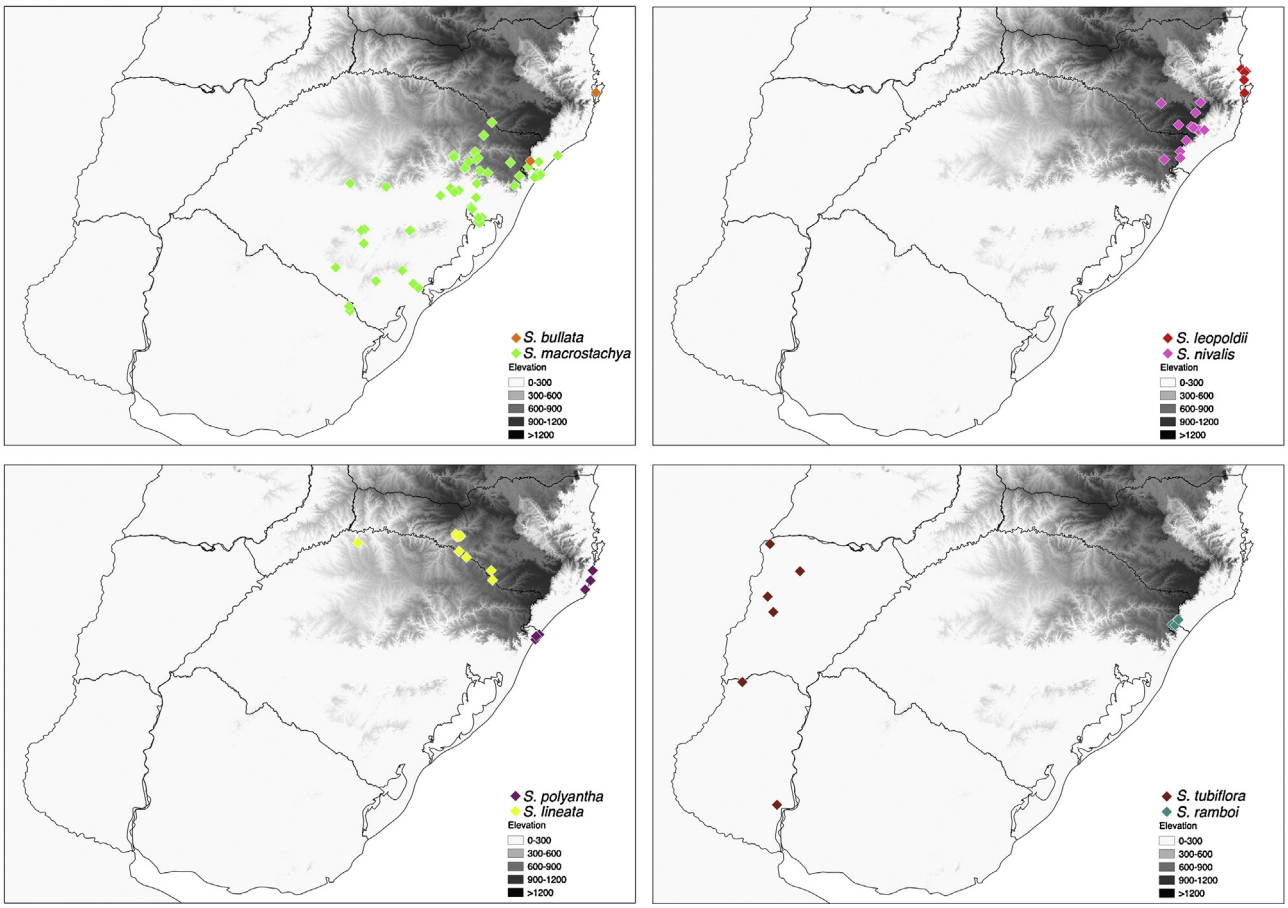

Fig. 3. Distribution of endemic subtropical *Sinningia* species in eastern subtropical South America.

be divided into spatial (latitude, elevation, distance from the coast), climatic (mean annual temperature, mean annual precipitation and number of frost days), and biogeographic (vegetation types). At a local scale, we differentiated soil types for terrestrial species, rock types for epipetric or rupestrial species, and bark types for epiphytic species. The number of classes or intervals considered for each of the potential factors varied from four (substrate types) to 12 (vegetation types), totalling 62 variables for each species. The number of occurrences in all environmental classes was interpreted as a measure of habitat tolerance for each species.

2.3. Data analyses

We used an exploratory multivariate approach to assess the contribution of the above mentioned variables on species' geographical and ecological distribution. To do so we merged continuous variables into intervals, and used minimum and maximum values for each variable, as well as the number of vegetation types in which a given species occurred and its classification as terrestrial, rupestrial and/or epiphytic. The resulting summarized data matrix (21 species described by 16 variables) was submitted to cluster and ordination analyses (Principal Coordinate Analysis) using Gower distance as a dissimilarity measure between species, and incremental sum of squares as a clustering criterion. We used Gower index because our data comprised multiple variable types, and PCoA was performed on the raw Gower matrix. Stability and significance of clustering groups and ordination axes were evaluated with bootstrap resampling methods (Pillar, 1998, 1999a,b). The 21 species were classified *a priori* into groups according to two criteria: phylogenetic group (*Dircaea* and *Corytholoma*) and geographic range (restricted and widespread). The robustness of this classification was tested using randomization tests with bootstrap resampling (Pillar and Orlóci, 1996). All randomization tests comprised 10,000 bootstrap iterations. We also searched for relationships between the southern limits of species ranges and climatic/habitat variables using Procrustes analysis (Peres-Neto and Jackson, 2001). In this analysis, we evaluated the pairwise congruence between variations in matrices containing information on species distribution (species described by latitude intervals) and climatic and habitat variables (species described by different categories/intervals according to each variable; see Appendix for raw matrices), using Euclidean distance as dissimilarity measure between sampling units (species).

Analyses were carried out with softwares Multiv (Pillar, 1997) and the R Platform (R Development Core Team, 2013).

3. Results

3.1. Distribution patterns

The 21 species of *Sinningia* belong to two clades, *Corytholoma* with seven species, and *Dircaea* with 14 species (Perret et al., 2003). Six species are widespread, four belonging to the clade *Corytholoma* and two to clade *Dircaea*. Among these species, *Sinningia allagophylla* showed the highest extent of occurrence, 483,000 km^2, followed by *Sinningia warmingii* with a smaller lesser extent of 96,000 km^2. The remaining species showed a restricted distribution, having less than 50,000 km^2 of extent of occurrence. Among the restricted species, some showed only a single collection point (Table 1), and so the extent of occurrence of 4 km^2 was attributed (Bachman et al., 2011). Most species occur near coastal plains or on the slopes of the Serra do Mar and Serra Geral. Only one species,

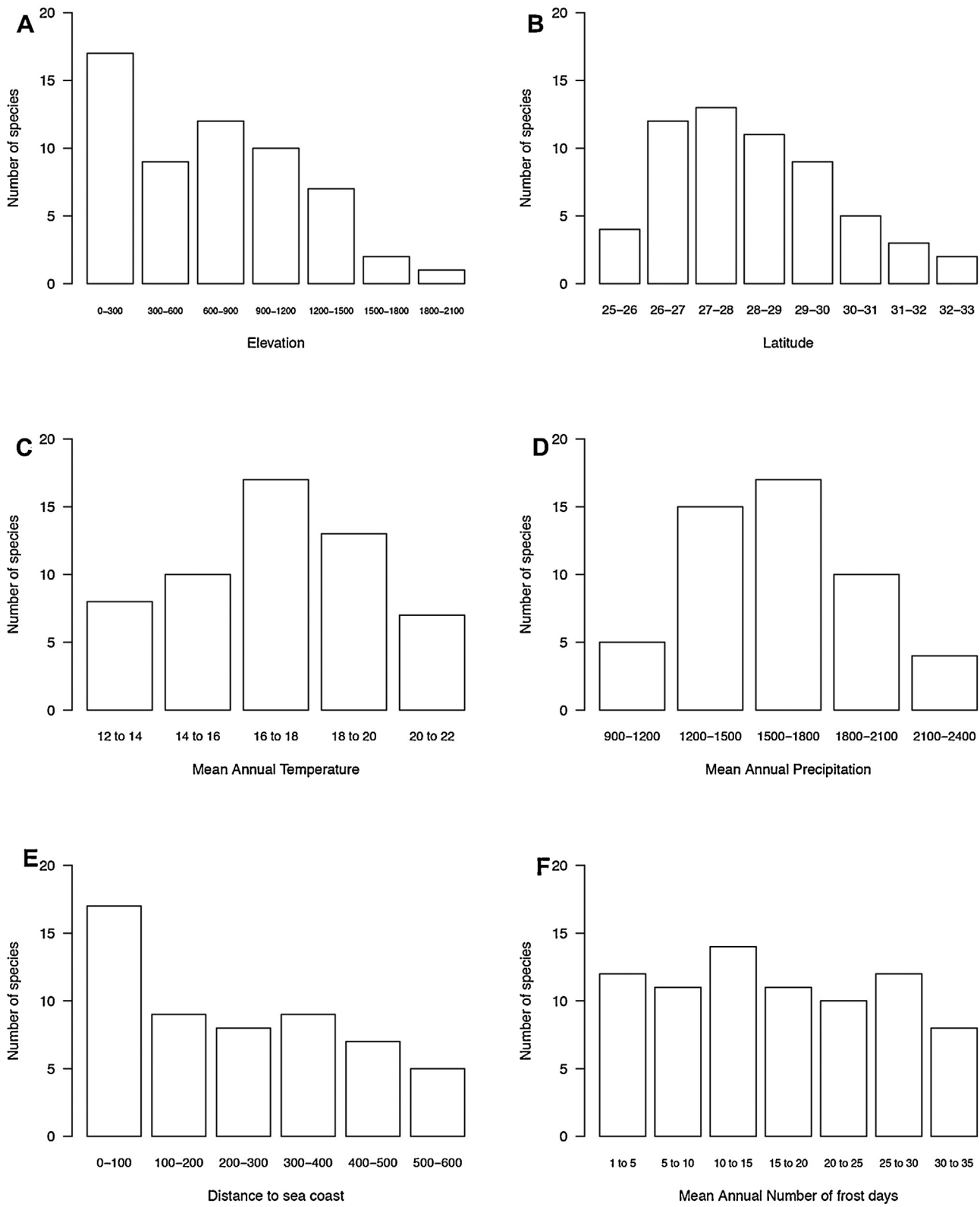

Fig. 4. Variation in the number of *Sinningia* species in relation to spatial and climatic variables.

Sinningia tubiflora presented a typical western distribution along the Paraná River plain (Fig. 2).

One third of the recorded species are endemics (36%), with important radiation in southeastern Santa Catarina (SC) and northeastern Rio Grande do Sul (Fig. 3). Among the eight endemic species, seven belong to the *Dircaea* clade and only one to the *Corytholoma* clade.

3.2. Ecological and geographic variables

According to spatial and climatic variables, species of *Sinningia* showed four distinct patterns (Fig. 4): (1) an overall decreasing tendency related to latitude and elevation, which are surrogates for temperature in the macroscale and mesoscale, respectively; (2) an outstanding species richness in one extreme situation of a gradient,

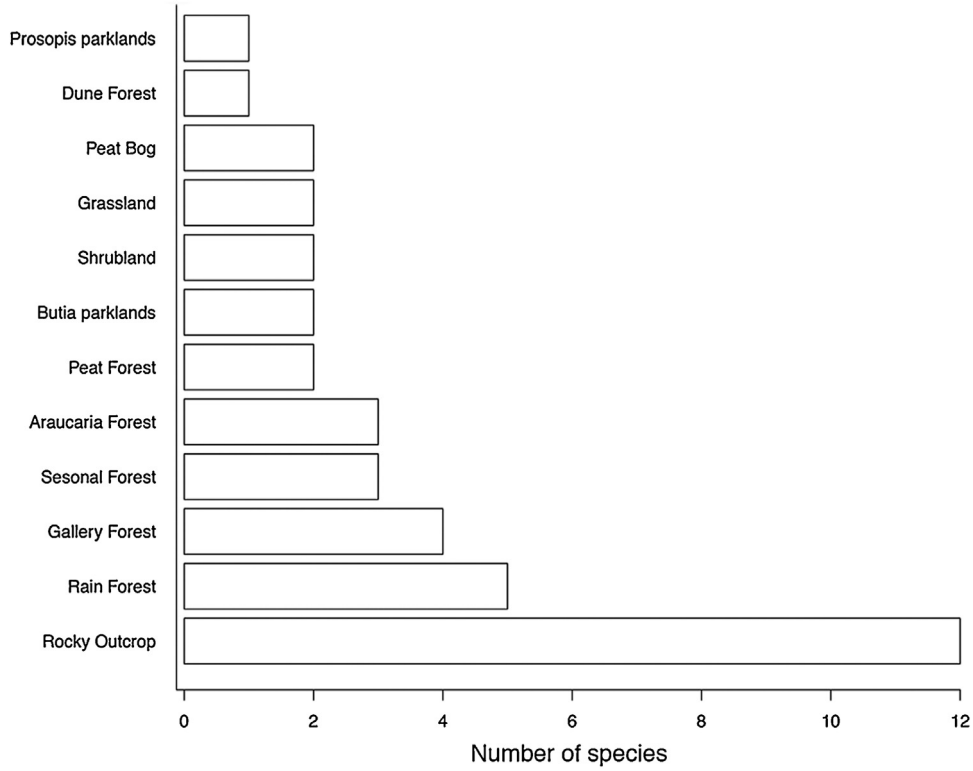

Fig. 5. Number of *Sinningia* species in major vegetation types in eastern subtropical South America.

Table 1
Geographic distribution and habitat of the *Sinningia* species (Gesneriaceae) occurring in the study area. Countries: AR = Argentina, BO = Bolivia, BR = Brazil, CO = Colombia, EC = Ecuador, PE = Peru, PY = Paraguay, UY = Uruguay, VE = Venezuela. Habit: T = terrestrial, R = rupestrial, E = epiphytic, H = helophytic, P = psammophytic, * = Southern Endemic Species.

Sinningia species	Code	Distribution	Habit	Extent of Occurrence (km^2)
S. aggregata (Ker Gawl.) Wiehler	aggr	BR, PY	R	41,041
S. allagophylla (Mart.) Wiehler	alla	AR, BR, PY, UY	T	483,283
S. bullata Chautems and M. Peixoto*	bull	BR	R	2037
S. conspicua (Seem.) G. Nicholson	cons	BR	T	4
S. cooperi (Paxton) Wiehler	coop	BR	E	308
S. curtiflora (Malme) Chautems	curti	BR	H	26,530
S. douglasii (Lindl.) Chautems	doug	AR, BR	ER	223,004
S. elatior (Kunth) Chautems	elati	AR, BO, BR, CO, PE, PY, UY, VE	H	277,431
S. hatschbachii Chautems	hats	BR	E	41
S. leopoldii (Scheidw. *ex* Planch.) Chautems*	leop	BR	R	264
S. leucotricha (Hoehne) H.E. Moore	leuc	BR	R	80
S. lineata (Hjelmq.) Chautems*	line	BR	R	13,239
S. macropoda (Sprague) H.E. Moore	macp	BR	R	4
S. macrostachya (Lindl.) Chautems*	macs	BR	R	105,718
S. nivalis Chautems*	nival	BR	RE	9575
S. polyantha (DC.) Wiehler*	poly	BR	P	1797
S. ramboi G.E. Ferreira et al.*	ramb	BR	RE	61
S. reitzii (Hoehne) L.E. Skog	reit	BR	R	8060
S. sellovii (Mart.) Wiehler	sell	AR, BO, BR, PY, UY	R	20,7960
S. tubiflora (Hook.) Fritsch*	tubi	AR, PY, UY	T	3,8850
S. warmingii (Hiern) Chautems	warm	AR, BR, EC, PE, PY	R	96,762

as shown by the higher number of species in coastal areas; (3) an almost constant or low varying richness along several environmental classes, as indicated by tolerance to the number of annual frost days; and (4) a non-monotonic hump shaped curve, suggesting more favourable conditions at intermediate intervals of a broader range, as evident in the relationship between species number and both mean annual temperature and mean annual precipitation.

The most common habitats type for subtropical *Sinningia* species are rocky outcrops, being these immersed or not in forests environments. In this habitat, the species are often associated to other xerophytic plants species, such as cacti, bromeliads and orchids, so that rocky outcrops can be regarded as vegetation types hosting a drought-adapted flora differing greatly from the surroundings. The number of species decreases exponentially towards other vegetation types (Fig. 5).

Habitat tolerance distinguished two species groups, separated by a larger discontinuity along the species rank according to the number of habitat classes (Fig. 5). One group was formed by six species occurring in 36–45 different habitats, and another formed by the remaining set of 15 species growing in 9–24 habitat classes.

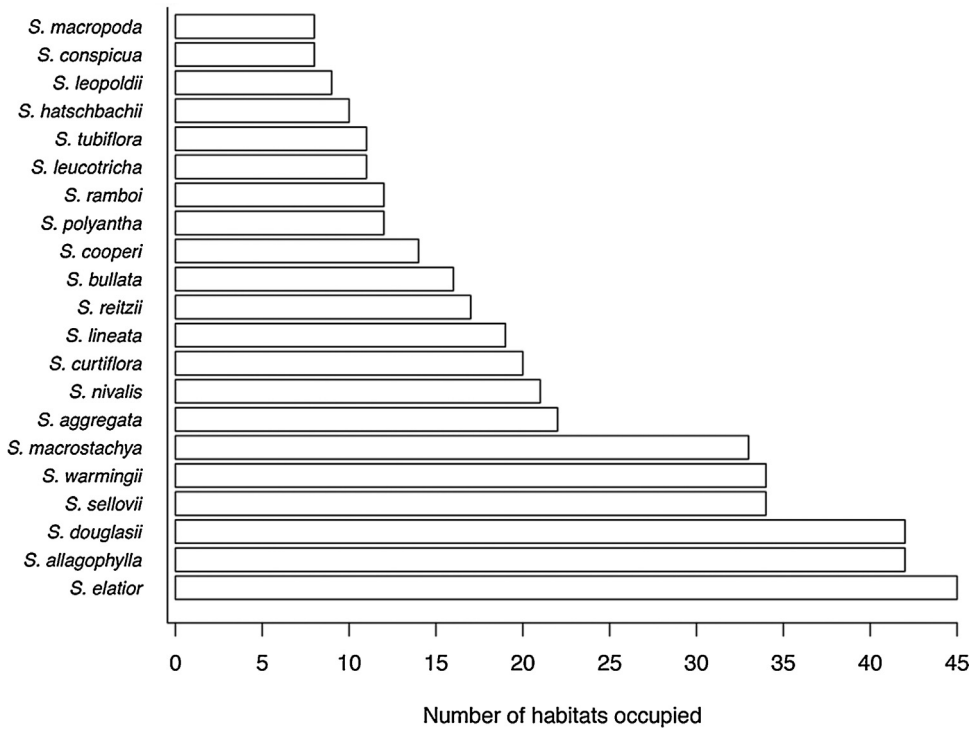

Fig. 6. Habitat tolerance in subtropical species of *Sinningia*. Two major groups can be distinguished, the more restricted species (above) and the more widespread species (below). Habitat tolerance was defined as the total number of conditions in which a given species occurs (see text for detailed explanation).

The first group was formed by four species classified in the clade *Corytholoma* (*S. elatior*, *S. allagophylla*, *S. sellovii* and *S. warmingii*), and two species included in the clade *Dircaea* (*S. douglasii* and *S. macrostachya*).

Ordination analysis showed a clear segregation between restricted and widespread species along axis 1, mostly defined by climatic variables, as well as a gradient of different habitat occupancy along axis 2 (Fig. 7). Species with broader geographical distribution concentrated on the left side of the ordination space, whereas more restricted species concentrated on the right side. Accordingly, cluster analysis resulted in two statistically significant groups of species comprising widespread and restricted taxa (cluster diagram not shown; $P > 0.2$). Variables with the highest correlation values with axis 1defined the segregation of widespread and restricted taxa in the ordination diagram: precipitation, temperature, frost days, latitude and distance from the Atlantic Ocean. Different preferences regarding habitat occupancy were depicted in a gradient along axis 2: from terrestrial taxa in the lower portion of the axis and rupestrial taxa in the upper portion, with epiphytic taxa as a transition in the middle. Although the distinction between species from different lineages was not significant ($P = 0.13$), the ordination diagram also showed a rough separation of lineages, with a great coincidence with geographical ranges. Most species in the *Dircaea* grouped on the left side of the diagram, except *S. macrostachya* and *S. douglasii*, which grouped with the species of the *Corytholoma* lineage on the right side of the diagram (Fig. 7). Procrustes analysis indicated significant congruence between the matrix describing the southern limits of species ranges and matrices containing the following variables: (i) mean annual precipitation (SQ = 0.3072; correlation = 0.8196; *p*-value = 0.0001), (ii) distance from the seacoast (SQ = 0.4557; correlation = 0.7098; *p*-value = 0.0001), (iii) mean annual temperature (SQ = 0.6687; correlation = 0.5806; *p*-value = 0.0016), and (iv) mean annual number of frost days (SQ = 0.7881; correlation = 0.5079; *p*-value = 0.0418).

4. Discussion

4.1. Distribution patterns and endemism

The genus *Sinningia* showed three different gradients of decreasing number of species according to all spatial variables analysed in this study: from (i) northern to southern latitudes; (ii) from lowlands to highlands and (iii) from coastal to inland regions (Figs. 4 and 7). These general trends were already identified for subtribe Ligeriinae (including *Vanhouttea* and *Paliavana*) by Perret et al. (2006), and for more general plant groups such as trees (Oliveira-Filho and Fontes, 2000) and bromeliads (Martinelli et al., 2008). Perret et al. (2006) also point out that the group originated in tropical forests along the São Francisco River in northeast Brazil and migrated southwards. In southern Brazil, the increasing distance from the ocean and the displacement to southern latitudes creates striking seasonal fluctuations in temperature and, below the 30°S parallel, the precipitation also diminishes gradually, which is mostly reflected by the dominance of grassland ecosystems (Soriano et al., 1989; Nery, 2005; Bilenca and Miñarro, 2004; Overbeck et al., 2007; Gonçalves and Souza, 2014).

Most species have a more or less continuous distribution within their range, whether it is restricted or widespread. According to present knowledge, only *S. conspicua* and *S. reitzii* (both from clade *Dircaea*) have a disjunct distribution. The former occurs from Minas Gerais to Santa Catarina but is absent in São Paulo. The latter occurs from São Paulo to Santa Catarina but was still not found in Paraná (Araujo et al., 2015). These occurrence gaps may be due to habitat destruction and replacement of natural vegetation by extensive areas with agricultural crops, but also because of lack of sampling in areas with difficult access along the Atlantic Rainforest. This may be particularly true for the rupestrial species growing on steep rocky escarpments, which is the case of most species of *Sinningia*.

The area between 27°S and 30°S parallels can be defined as a subtropical centre of endemism of *Sinningia*, which coincides with

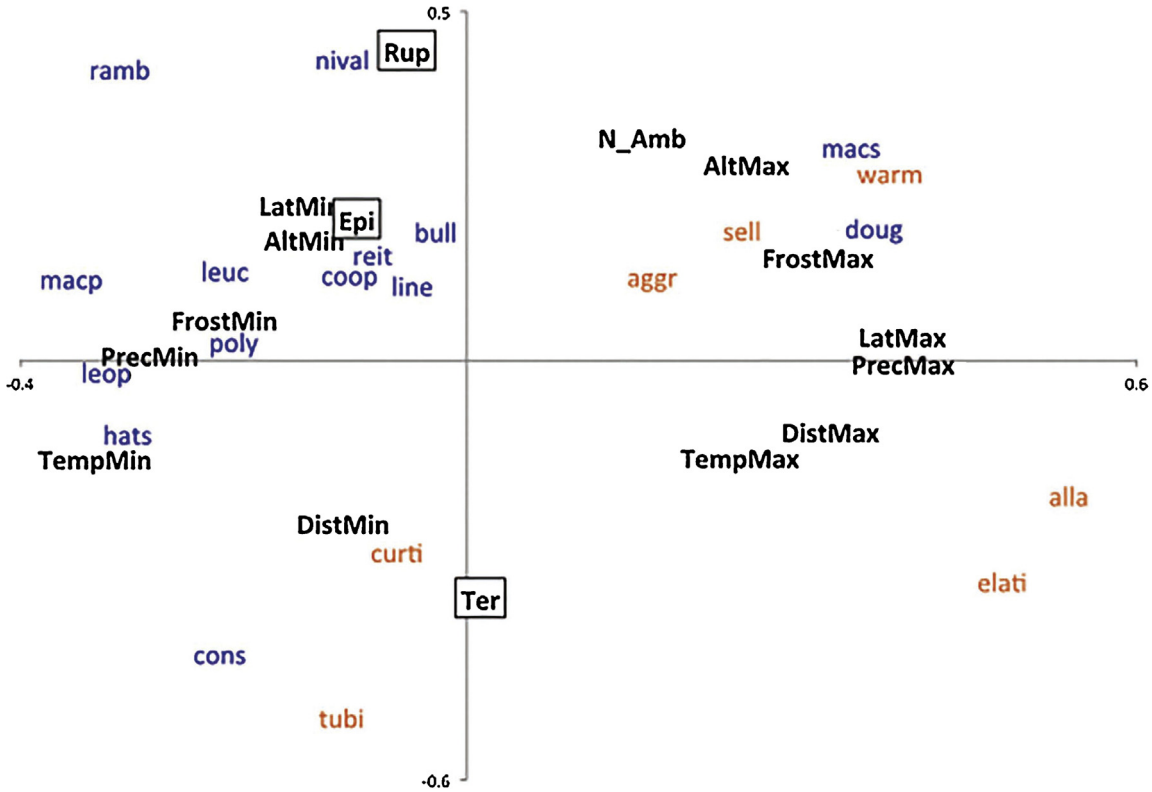

Fig. 7. Principal coordinate analysis (PCoA) showing *Sinningia* species (see acronyms on Table 1) and environmental factors. Species in clade *Dircaea* are shown in blue whereas those in clade *Corytholoma* are shown in orange. Legend: AltMin – Minimum altitude; AltMax – Maximum altitude; LatMin – Minimum latitude; LatMax – Maximum latitude; DistMin – Minimum distance; DistMax – Maximum distance; TempMin – Minimum temperature; TempMax – Maximum temperature; FrostMin – Minimum frost day; FrostMax – Maximum frost day; PrecMin – Minimum preciptation; PrecMax – Maximum preciptation; NoAmb – Number of environments; Ter – Terrestrial; Rup – Rupestrial; Epi – Epiphytic.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the border between southern Santa Catarina and northeastern Rio Grande do Sul (Fig. 2). In this area, seven of the eight endemic *Sinningia* species were found (Fig. 3). This region presents a marked altitudinal gradient, from the sea level to mountains with up to 1800 m, with a great variety of vegetation types and a high diversity of habitats. Also, the region is located outside the Atlantic Rainforest and its historically stable areas (Carnaval and Moritz, 2008), because of the large vegetation changes that took place since the Last Glacial Maximum-LGM (Behling et al., 2004; Jeske-Pieruschka et al., 2011). The sites that had a long-term environmental stability (refugia) may have accumulated species, which is corroborated by present biodiversity (Carnaval et al., 2009). Also, the changing landscape and climate, ecological gradients and elevated number of habitats may promote speciation events and the resulting increased biodiversity (Rabosky et al., 2012; Hoorn et al., 2013). However, if refuges had occurred it would be expected that species diverged earlier (relict species), which is not the case in this study, since the species of *Sinningia* are the result of recent speciation events at about 3 Mya (Perret et al., 2013).

4.2. Limiting factors

The overall species richness decrease related to latitude and elevation, as well as the distance from the coast, indicates that the low winter temperatures and unstable climate are limiting the distribution and overall species richness in subtropical *Sinningia* species. It is important to consider that subtribe Ligeriinnae originated in the Atlantic Rainforests along the São Francisco region in northeastern Brazil (Perret et al., 2006, 2013), and the distance between the center of origin of this taxon and southern Brazil may be a second factor contributing to the rather low diversity of the tribe in this region. Recent findings on the origin of this species corroborate this argument (Perret et al., 2013), and similar results were found by Fontoura et al. (2012) for Bromeliaceae from the Atlantic Rainforest.

A high number of species occur in the Atlantic and Paranean biogeographic provinces, both associated with the mostly forested Amazonian domain (Cabrera and Willink, 1980). The 30°S parallel represents a striking floristic and vegetational transitional region in South America. In the study area around this parallel, the forest types of the Atlantic and Paranean provinces more or less abruptly change to grasslands and parklands of the Pampean and Espinal biogeographic provinces (Fig. 1), both associated with the Chacoan domain (Cabrera and Willink, 1980; Waechter, 2002).

We have found a great overlap between biogeographic ranges (broad and narrow species) and phylogenetic groups (*Corytholoma* and *Dircaea* clades). As expected, the species with a widespread distribution were also those with the greatest range of habitats occupied, whereas restricted species showed overall lower habitat tolerance (Fig. 6). Restricted-range species were also closely related to variables such as maximum altitude, frost days, precipitation and distance from the ocean (Fig. 7), which could indicate a set of environmental constraints to range expansion that these species may share. Results from Procrustes analysis also point out towards this set of constraining variables, indicating that precipitation, temperature, number of frost days and distance from the seacoast play an important role on range extent, at least considering a North-South variation.

However, divergence time may also play an important role for range restriction in these lineages. The species with the widest distribution and environmental tolerance are those of the *Corytholoma* lineage, an early-divergent clade within genus *Sinningia*

(ca. 14 Mya) in comparison with the *Dircaea* lineage. The remaining species are those of the *Dircaea* lineage, a clade that diverged later, ca. 10 Mya (Perret et al., 2013). The species in *Corytholoma* have the widest geographical and ecological distribution possibly because they have had more time to expand their distribution and to colonize a larger number of environments in comparison with *Dircaea* species. Interestingly, only two species in this clade, namely *S. douglasii* and *S. macrostachya*, have a relatively wide ecological amplitude (Figs. 6 and 7), and this may be due to an early divergence within the clade. On the other hand, *S. curtiflora* and *S. tubiflora*, both in the clade *Corytholoma*, have a relatively lower habitat tolerance and diverged late within the clade. However, we do not claim that divergence time alone defines range extent in these lineages. It is likely that phylogeny and ecological preferences (and possibly other factors we did not include in this study) jointly shape their present biogeography.

5. Conclusions and perspectives

Our results lead us to believe that the ecological and geographical distribution patterns of subtropical *Sinningia* species are strongly related to (i) climatic constraints such as low tolerance to low temperatures and larger climatic fluctuations outside the coastal plain, and (ii) the evolutionary history of the genus. The southern boundary of several tropical or widespread species is probably related to climatic changes around the 30°S parallel. In this region the forested Atlantic and Paranean biogeographic provinces rather abruptly change into the non-forested Espinal and Pampean provinces. The relatively high diversity of this genus in the South American subtropical region, which can be seen as a regional centre of endemism, is a result of relatively high habitat heterogeneity. Future research focused on the biogeographical history of *Sinningia* should include more taxa in order to expand the results we presented here to a broader geographical extent. Including more variables such as species' functional traits may also contribute to the understanding of distribution patterns and the evolutionary history of the group.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.flora.2016.04.002.

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